

effect of mixing equal volumes of hydrogen and helium, each of which has too large a coefficient of elasticity, is to cause each to occupy twice the volume that they previously occupied, and to halve approximately the pressure for each. The pressure is therefore lower than it would be for an absolutely ideal gas, for each gas, hydrogen and helium. The sum of these pressures will accordingly be too low, or transposing, the sum of the volumes will be too great. The opposite argument holds for air.

Now, in considering volumes we deal not merely with the co-volume, *i.e.*, the space occupied by the molecules, but also with the interstitial space inhabited by the molecules. But the refractive power, if Clausius's deduction from the formula of Lorenz and Lorentz is correct, is a function of the dielectric constant, and hence of the co-volumes of the gases. And here the discrepancy is more easily detected than by any determination of density. It must therefore be concluded that gases are not, as postulated by Dalton, indifferent to one another's presence, but that they modify one another's properties in the same manner as do liquids, though to a different extent. This mutual action at high pressures and small volumes modifies even the volume relations, as recently shown by Dr. Kuenen. And it must persist at low pressures and large volumes, though it may not always be possible to make measurements of pressure and volume accurate enough to lead to its detection. The refractivity, however, seems to be a means delicate enough to be used for this purpose.

“On the Openings in the Wall of the Body-cavity of Vertebrates.” By EDWARD J. BLES, B.Sc. (Lond.), King's College, Cambridge. Communicated by Dr. HANS GADOW, F.R.S. Received June 16,—Read June 17, 1897.

In the review of the vertebrates held in the following pages, I have put together as many facts as I could ascertain on the distribution of abdominal pores in the various groups, and side by side with this evidence I have arranged the available facts recorded by others, and observed by myself, on the distribution of nephrostomes and other openings on the wall of the abdominal cavity.

By so doing, the physiological meaning of the abdominal pores has, I believe, been elucidated through the evidence of a correlation, speaking generally, of an alternative character, between these two sets of organs. It will further appear that in most of the higher vertebrates —where abdominal pores do not occur and nephrostomes disappear early in development or lose their original connection with the renal ducts—the body-cavity has taken upon itself a different functional character. Instead of acting as auxiliary to the excretory organs, it takes part in the internal work of the circulatory lymphatic system.

The greater part of the information on the openings from the perivisceral cavity to the exterior in the Elasmobranchii is contained in two papers; one by Semper,* on the urogenital system of Plagiostomes, the other, by Bridge, on "Pori Abdominales of Vertebrata."† Semper describes the persistence in certain Elasmobranchs of a number of open segmental funnels on the peritoneal epithelium leading into the Malpighian bodies of the mesonephros. Such funnels occur in all Elasmobranch embryos, but usually close during development. Semper gives lists of species with and without nephrostomes when adult, and shows that their presence cannot be correlated with the presence or absence of other organs, among which he did not, however, refer to the abdominal pores. Bridge was the first to examine a number of Elasmobranchs expressly to determine the distribution of abdominal pores amongst the species of these fishes. He states that it was "not clear that the presence or absence of the pores can be correlated with structural variations in other organs." I was led to compare Semper's and Bridge's accounts of the distribution of nephrostomes and abdominal pores, and it at once became evident that their presence in Elasmobranchs was, to a certain extent, reciprocal. A few discrepancies which appeared have been investigated, and my results, although they agree in the main with Bridge's, differ from his in one or two important cases. A detailed discussion of these cases will appear elsewhere.

The species which have come under my own observation are:—
Carcharias acutus, Rüppel, *C. glaucus*, L., *Galeus canis*, Bonap., *Zygaena malleus*, Risso, *Mustelus vulgaris*, M. and H., *M. levis*, Risso, *Hexanchus griseus*, Gm., *Heptanchus cinereus*, Gm., *Scyllium canicula*, L., *S. stellare*, L., *Pristiurus melanostomus*, Bonap., *Cestracion philippi*, Lacép., *Spinax niger*, Bonap., *Scymnus lichia*, Cuv., *Centrophorus granulosus*, Bl. Schn., *Rhina squatina*, L., *Pristiophorus cirratus*, Lath., *Pristis zyson*, Blkr., *Rhinobatus djeddensis*, Forsk., *Rhinobatus granulatus*, Cuv., *Torpedo narce*, Risso, *Narcine brasiliensis*, Olf., *Raja clavata*, L., *R. maculata*, L., *Myliobatis maculata*, Gray, and *Myli. sp.*

Table I contains all the species for which there are data respecting both nephrostomes and abdominal pores. It includes all the species investigated by Semper, excepting *Lamna glauca*, M. and H., and *Temera hardwickii*, Gray. In these two species the nephrostomes close, and it may be expected that they will eventually be found to possess abdominal pores.

Table II is so arranged that the species with nephrostomes are

* C. Semper, "Das Urogenitalsystem der Plagiostomen und seine Bedeutung für das der übrigen Wirbelthiere," 'Arb. Zool.-zoot. Inst. Würzburg,' vol. 2 (1875), pp. 195—509.

† 'Journ. Anat. and Phys.,' vol. 14 (1879), pp. 81—100.

placed together under A, and the species without them together under B. The species under B all possess abdominal pores. Under A, on the other hand, there is no such uniformity as regards the pores. We have here a fairly complete series of species; beginning with forms without abdominal pores like *Cestracion*, passing to forms like *Scy. stellare*, which acquire pores late in life and may occasionally fail to do so; we then come to the *Scy. canicula* group, where pores are found at the stage of sexual maturity, but where they may be acquired still later or sometimes not at all; and, lastly, there is a fourth group, that of *Acanthias vulgaris*, where the pores appear at an early age, towards the end of embryonic life, and seem to be invariably present. These four groups have one character in common: the nephrostomes remain open in the adult. In this they differ from the species under B, which close the nephrostomes early in development, and then, like Group 4 of Series A, and likewise at an early age (*Carcharias* during foetal life), open abdominal pores.

To some of the species in Table I no place in Table II can be assigned until more specimens of different ages have been examined.

It is sufficiently obvious from the list of species in Series B of Table II that abdominal pores are distributed without reference to oviparity or viviparity.

Table I.
Elasmobranchii.

	Segmental tubes.		Abdominal pores.	
	Open.	Closed.	Present.	Absent.
Sub-Order SELACHOIDEI.				
Fam. 1. <i>Carchariidae.</i>				
a. <i>Carchariina.</i>				
<i>Carcharius glaucus</i> , L.	—		+	
<i>Galeus canis</i> , Bonap.	—		+	
b. <i>Zygennina.</i>				
<i>Zygæna malleus</i> , Risso, ♂				
juv.	—		+	
c. <i>Mustelina.</i>				
<i>Mustelus vulgaris</i> , M and				
H.	—		+	
<i>M. lævis</i> , Risso, ♀	—		+	
<i>Triakis semifasciata</i> , Girard	—		+	
Fam. 2. <i>Lamnidæ.</i>				
<i>Lamna cornubica</i> , Gm.	—		+	
(Fam. 3. <i>Rhinodontidæ.</i>)				
Fam. 4. <i>Notidanidæ.</i>				
<i>Hexanchus griseus</i> , Gm., ♀ juv.	+		+	
<i>Heptanchus cinereus</i> , Gm., ♀ ..	+		(or +)	—

Table I—continued.

	Segmental tubes.		Abdominal pores.	
	Open.	Closed.	Present.	Absent.
Sub-Order SELACHOIDEI—cont.				
Fam. 5. Scyliiidæ.				
<i>Scylium canicula</i> , L., ♂, 7 cases (E. J. B.)	+		+ (5 cases)	— (2 cases)
Ditto, ♂ (Bridge)	+		+	—
Ditto, ♂ (Marshall and Hurst)	+		+ (6 cases)	— (6 cases)
Ditto, ♀, 12 cases (E. J. B.)	+			—
Ditto, ♀ (Bridge)	+		+	—
Ditto, ♀ (Marshall and Hurst)	+		+	—
Ditto, ♀ juv., (ditto)	+			—
<i>Scylium stellare</i> , L.	+		(or +)	—
<i>Pristiurus melanostomus</i> , Bonap.	+		(or +)	—
Fam. 6. Cestraciontidæ.				
<i>Cestracion philippi</i> , Lacép., ♀	+			—
Fam. 7. Spinacidæ.				
<i>Centrina salviani</i> , Risso, ♀	?	+		+
<i>Centrophorus granulosus</i> , Bl. Schn.	+			+
Ditto, ♂ juv.	+			—
<i>Scymnus lichaia</i> , Cuv.	+			+
<i>Acanthias vulgaris</i> , Risso	+			+
Ditto, 12" fœtus (Bridge)	+			—
<i>Spinax niger</i> , Bonap., ♂	+			—
Ditto, ♀	+			(or —)
Fam. 8. Rhinidæ.				
<i>Rhina squatina</i> , L.	+			—
(Fam. 9. Pristiophoridæ.)				
Sub-Order BATOIDEI.				
(Fam. 1. Pristidæ.)				
Fam. 2. Rhinobatidæ.				
<i>Rhinobatus djeddensis</i> , Forsk., ♀	—		+	
<i>Rhinobatus granulatus</i> , Cuv.	—		+	
Fam. 3. Torpedinidæ.				
<i>Torpedo narce</i> , Risso	—		+	
" <i>marmorata</i> , Risso	—		+	
<i>Hypnos subnigrum</i> , Dum., ♂	—		+	
<i>Narcine brasiliensis</i> , Olf.	—		+	
Fam. 4. Rajidæ.				
<i>Raja clavata</i> , L.	—		+	
" <i>maculata</i> , Montag., 10 cases (E. J. B.)	—		+	
" <i>punctata</i> , Risso	—		+	
" <i>miraleetus</i> , L.	—		+	
" <i>batis</i> , L.	—		+	
" <i>marginata</i> , Lacép.	—		+	
" <i>blanda</i> , Holt and Calder-wood	—		+	
Fam. 5. Trygonidæ.				
<i>Trygon bruceo</i> , Bonap.	—		+	
" <i>pastinaca</i> , L.	—		+	
Fam. 6. Myliobatidæ.				
<i>Myliobatis maculata</i> , Gray, ♀	—		+	
" <i>sp.</i> , ♀ juv.	—		+	

Table II.

A. Elasmobranchs with nephrostomes when adult.

- (1) Abdominal pores absent.
 - Cestraciontidæ. *Cestracion philippi*, Lacép.
 - Rhinidæ. *Rhina squatina*, L.
- (2) Abdominal pores absent until full-grown. (Whether they are then constantly present is not known.)
 - Scyliiidæ. *Scylium stellare*, L.
Pristiurus melanostomus, Bonap.
- (3) Abdominal pores appear late (when sexually mature) and may be absent.
 - Scyliiidæ. *Scylium canicula*, L.
 - Spinacidæ. *Spinax niger*, Bonap.
- (4) Abdominal pores appear early and are constantly present.
 - Spinacidæ. *Acanthias vulgaris*, Risso.
Symnus lichia, Cuv.

B. Elasmobranchs without nephrostomes when adult.

- (5) Abdominal pores always present.
 - SELACHOIDEI. Carchariidæ. *Carcharias glaucus*, L. *Galeus canis*, Bonap., *Zygæna malleus*, Risso, *Mustelus vulgaris*, M. and H., *M. lærvis*, Risso, *Triakis semifasciata*, Girard.
 - Lamnidæ. *Lamna cornubica*, Gm.
 - BATOIDEI. Rhinobatidæ. *Rhinobatos djeddensis*, Forsk.
Rhinobatos granulatus, Cuv.
 - Torpedinidæ. *Torpedo narce*, Risso, *T. marmorata*, Risso, *Hypnos subnigrum*, Dum., *Narcine brasiliensis*, Olf., *Raja clavata*, L., *R. maculata*, Montag., *R. blanda*, Holt and Calderwood, *R. punctata*, Risso, *R. miraletus*, L., *R. batis*, L., *R. marginata*, Lacép.
 - Trygonidæ. *Trygon brucei*, Bonap.
T. pastinaca, L.
 - Myliobatidæ. *Myliobatis maculata*, Gray,
Myliobatis sp.

The most obvious of the facts brought into prominence by the above tables are the following:—

1. The Elasmobranch fishes when adult have a peritoneal cavity which in every known instance communicates with the exterior.
2. This communication is established in several ways:—
 - (a) Through nephrostomes and urinary canals;
 - (b) More directly, through abdominal pores; but
 - (c) Both communications may exist together in the same individual.
3. Disregarding for the moment the eight species which, roughly speaking, possess both sets of openings, there remain twenty-eight species in which a correlation of an alternative nature

exists between the renal communications on the one hand and the abdominal pores on the other. There are four species with persistent nephrostomes and practically without abdominal pores, and twenty-four species with abdominal pores which lose the nephrostomes very early in development.

4. The Batoidei and the Carchariidæ are characterised by the absence in the adult of open nephrostomes and the presence of abdominal pores.

In the above statements no account has been taken of the third channel of communication present in all female Elasmobranchs, that practicable through the oviduct after the disappearance of the hymen.

The relations thus brought to light afford a fairly complete account of the distribution of both nephrostomes and abdominal pores amongst adult Elasmobranchs. The total number of species (thirty-six) from which these conclusions have been drawn is somewhat small when compared with the number of species on record in this group, viz., more than 300. The families of the group are, however, all represented, with the exception of the Rhinodontidæ, the Pristiophoridæ, and the Pristidæ, in which nothing is known of the nephrostomes; but I found abdominal pores in a species from each of the Selachian and Batoid families of Sawfishes. It follows then that with the two species referred to and six additional species from various families of Selachians known to possess abdominal pores,* there are forty-four species in which the abdominal cavity is known to communicate with the exterior, and not one in which this cavity is shut off from such communication. So that we may extend the generalisations arrived at from the discussion of the material here brought together to the whole of the Elasmobranchii. It may hence be concluded that the body cavity of adult Elasmobranchs is never completely enclosed by the peritoneum; it always communicates with the exterior, the communication being effected in various ways, as shown above.

The distribution of species with nephrostomes and of species without them in the Elasmobranchii is clearly shown in Table I. The scheme of classification adopted is from Dr. Günther's ' Catalogue of Fishes in the British Museum ' (published in 1870).

A glance at Table I shows that the Carchariidæ all close the segmental tubes, three species of Scyliiidæ retain them, four, probably five, species of Spinacidæ do the same; also two species of

* These eight species are:—*Pristis zysron*, Blkr., *Pristiophorus cirratus*, Lath., *Echinorhinus spinosus*, Gm., *Læmargus borealis*, Scoresb., *Chlamydoselachus anguineus*, Garm., *Zygæna tudes*, Cuv., *Carcharias melanopterus*, Q. and G., and *Carcharias acutus*, Rüppel.

Notidanidæ do so; while all the Batoidei lose the peritoneal nephridial openings. Thus the classification here employed is in harmony with the distribution of nephrostomes in adult Elasmobranchs.

Table III.—In this table I have placed, side by side, the data respecting the distribution of nephrostomes and of abdominal pores in all the Vertebrates not yet dealt with, excluding the Cyclostomes. The latter are omitted on account of the great probability that the so-called abdominal pores of Cyclostomes are genital ducts, morphologically as well as functionally, and hence quite distinct from true abdominal pores, which are never used as genital ducts.

The fishes in which the ova when mature fall into the general body cavity usually have abdominal pores; this applies to certain Elasmobranchs, the Holocephala, most Ganoids, some Dipnoi, and to some Salmonidæ. But there are exceptions, as we have seen, amongst the Elasmobranchs; some Salmonidæ have no pores, and other Teleosteans with the primitive form of ovary have none, e.g., Murænidæ, Galaxidæ, &c. Then, on the other hand, there are fishes with tubular closed ovaries forming a continuous tube with the oviducts and with a lumen quite distinct from the body-cavity, as it is in the majority of Teleosteans, yet the body-cavity is, nevertheless, open to the exterior through abdominal pores. *Lepidosteus osseus* is in this condition, and, amongst Teleosteans, the Mormyridæ. It follows that there is no correlation between the condition of the ovary and the occurrence of abdominal pores.

It is noteworthy that in the Amphibia alone, amongst the Vertebrates ranking higher than Elasmobranchs, do the nephrostomes persist in the adult, and that the abdominal pores are entirely absent. This is the more striking, since the abdominal pores reappear in Reptiles, in the absence of nephrostomes.

Equally important, from the present point of view, is the change of function of the nephrostomes within the group Amphibia. In the Gymnophiona and Urodela the original excretory function is served; but in Anura, where the lymphatic system is more highly developed, the body-cavity has become a lymph space, and the nephrostomes lead from it directly into the renal veins, not into the kidney tubules (Nussbaum). The abdominal cavity of Anura is also, through the stomata, in close communication with the lymphatic system, and so, through the lymph-hearts, with the veins. Hence the body-cavity of the lower Amphibia may be compared, as regards its relations to the kidneys, with the body-cavity of certain Elasmobranchs (Cestracion), while the relations of body-cavity and vascular system in the Anura are parallel to those obtaining in the higher Reptilia and in Mammals.

Table III.

	Segmental tubes.		Abdominal pores.	
	Open.	Closed.	Present.	Absent.
HOLOCEPHALA.				
<i>Chimaera monstrosa</i>		—	+	
GANODET.				
<i>Lepidotes osseus</i>	(? + into lumen of ovary) Balfour and Parker.	— in peritoneal cavity.	+ (Joh. Müller, Hyrtl).	
Sturiones		— (<i>Acc. sturio</i> , Jungersen)	+ (Joh. Müller, Hyrtl).	
<i>Polyodon folium</i>			+ (A. Wagner, Hyrtl).	
<i>Polypterus bichir</i>			+ (Hyrtl).	
<i>Catamarcichthys celataarius</i>			+ (Bridge).	
<i>Amia calva</i> , adult		— (Jungersen).	+ (Hyrtl, Bridge).	
” ”, larvæ, 16½ mm.	+ (Jungersen).	— (Jungersen).	— (Jungersen).	
DIPNOI.				
<i>Protopterus annectens</i>		— (Parker, Wiedersheim).	+ (Owen, Stannius).	
<i>Ceratodus forsteri</i>		(? — Ehlers).	+ (Günther).	
<i>Lepidotes paradoxus</i> , Fitz.		(? — Ehlers).	— (Hyrtl).	
TELEOSTEI.				
Salmonidae.				
<i>Argentina silus</i> , Risberg		—	+ (M. Weber).	
<i>A. hebridaica</i> , Yar. spec.		—	+	”
<i>Coregonus lavaretus</i> , L.		—	+	”
<i>Salmo trutta</i> , L., ♂		—	+	”
<i>Coregonus oxyrinchus</i> , ♂		—	+	”
” ”, ♀		—	+	”
<i>Salmo fario</i> , L.		—	+	”
<i>Salmo salar</i>		—	+	”
” ”, juv.		—	+	”
<i>Osmurus opercularis</i> , L.		—	— (M. Weber).	
<i>Mallotus villosus</i> , Quay.		—	— ”,	

Table III—*continued.*

	Segmental tubes.			Abdominal pores.	
	Open.	Closed.	Present.	Present.	Absent.
TELEOSTEI—continued.					
Mormyridæ.					
<i>Mormyrus oxyrhynchus</i>	—	—	+	(Hyrtl).	
" <i>bane</i>	—	—	+	"	
" <i>epipinnoides</i>	—	—	+	"	
" <i>elongatus</i>	—	—	+	"	
" <i>dorsalis</i>	—	—	+	"	
" <i>anguillaris</i>	—	—	+	"	
" <i>zambezensis</i>	—	—	+	"	
" <i>caschive</i>	—	—	+	"	
<i>Gymnarchus niloticus</i>	—	—	+	"	
All remaining Teleostei	—	—	—		
(In ♀ Muranide, Galaxide, Hyodontidae, Bathythrisidae, and Notopteridae the body cavity opens to the exterior through the oviducts.)					
AMPHIBIA.					
<i>Gymnophiona</i>	+	+	+		
<i>Urodela</i>	+	+	+		
<i>Anura</i>	+	+	(open into the renal veins).		
REPTILIA.					
<i>Hatteria</i>	—	—	(Wiedersheim).		
<i>Chelonia</i> .	—	—			
<i>Geomyda grandis</i> , ♂	—	—	(Vestiges, Gadow).		
			+ (Anderson).		

<i>Enyalius hamiltonii</i> , ♂	+	—	—	—	—	—
<i>Trionyx ocellatus</i> , ♂	+	+	—	—	—	—
" <i>gangesiensis</i> , ♀	+	+	—	—	—	—
<i>Batagur thuragi</i> , ♀	+	+	—	—	—	—
<i>Chitra indica</i> , ♀	+	+	—	—	—	—
<i>Enyalius trivaga</i> , ♀	+	+	—	—	—	—
<i>Testudo platynotus</i> , ♀	+	+	—	—	—	—
<i>Batagur lineatus</i> , ♀	+	+	—	—	—	—
<i>Testudo microphyes</i> , ♂	—	—	—	—	—	—
" <i>elephantopus</i> , ♂	—	—	—	—	—	—
" <i>græca</i> , ♂	—	—	—	—	—	—
" <i>nemoralis</i> , ♂	—	—	—	—	—	—
<i>Chelone midas</i> , ♂	—	—	—	—	—	—
" ♀	—	—	—	—	—	—
<i>Crocodilia</i>	—	—	—	—	—	—
<i>Crocodilus vulgaris</i>	—	—	—	—	—	—
<i>Alligator</i> sp., ♂ and ♀	—	—	—	—	—	—
<i>Crocodilus</i> sp., ♂	—	—	—	—	—	—
<i>Lacertilia</i>	—	—	—	—	—	—
<i>Lacerta</i> and <i>Anguis fragilis</i>	—	—	—	—	—	—
have stomata on peritoneum.)						
<i>Opisthida</i>	(These groups have apparently not been examined for the presence of stomata.)					
MAMMALIA	(Stomata are present both on the pleural and abdominal serous membranes.)					

Conclusions.

The first inference to be drawn from the facts as here presented is one bearing on the function of the abdominal pores. When some conclusion has been reached as to whether the pores are mere vestigial rudiments of no present physiological value, or whether they are of real functional value to those vertebrates in which they occur, then an attempt may be made to assign to them their morphological meaning.

The opinion held by Bridge as the result of his investigations on abdominal pores was, that, excepting in those cases where the genital products passed out through them, they had no definite function. It is now known that true abdominal pores do not serve as genital ducts; the so-called abdominal pores of Cyclostomes, Murænidæ, &c., are really genital ducts, and their homologies do not point to the abdominal pores of the Elasmobranchs, &c. The pores would, accordingly, be left without any particular function.

This conclusion is, I believe, contradicted by the facts connected with the relative distribution of nephrostomes on the one hand and abdominal pores on the other. In the Elasmobranchs three larger groups may be recognised. In one nephrostomes only occur, in another abdominal pores only, in the third nephrostomes are always present, while abdominal pores may or may not be added. Amongst the Holocephala abdominal pores alone exist in the adult *Chimæra monstrosa*. The Ganoids lose their nephrostomes, but all have abdominal pores. All that is clear about the Dipnoi points to the presence of abdominal pores in *Ceratodus* and in *Protopterus annectens*, nephrostomes being absent. The Teleostei with abdominal pores have no nephrostomes. The Amphibia Cæcilia and the Amphibia Urodela both have nephrostomes opening a passage from body-cavity to the exterior. In certain Chelonia and Crocodilia, which close their nephrostomes during embryonic life, abdominal pores are present. All the groups just mentioned have either nephrostomes or abdominal pores, or in some (intermediate) cases both together. In none are both openings absent, and it appears to be necessary for some passage to be open between the body-cavity and the exterior. This consideration gives, I believe, a clue to the function of the abdominal pores. As they alternate on the whole in their distribution with the nephrostomes, they undertake in all probability the duties of the absent nephrostomes, or when both are present together they act in mutual support of each other.

In what the function of the pores chiefly consists is demonstrated by a very interesting experiment recently performed by Guido Schneider.* He injected finely divided Indian ink mixed

* 'Anat. Anz.' vol. 13, No. 15, p. 393.

with a little carmine into the body-cavity of specimens of *Squatina angelus* (*Rhina squatina*, L.). Two days later the animals were killed. Phagocytes laden with the colouring matter were found in the nephrostomial funnels and in spaces in the kidney into which these funnels led. Whether these spaces were continuous with the lumen of the renal tubules could not be determined. But in addition to this means of clearing the foreign matter away from the peritoneal cavity, another method, as I take it, appears to have been resorted to. I have satisfied myself that in the normal *R. squatina* there are no abdominal pores, but there are cloacal pits with exceedingly thin walls towards the body-cavity. From Schneider's description, I conclude that these walls were broken through in his more or less pathological specimens, forming ruptures on each side of the cloacal slit. They appeared as black pits pigmented with Indian-ink-laden leucocytes, wandering, as he explains, into the tissue round the pore. The pigmented leucocytes were found only in these two places, and the pores had opened, no doubt, I consider, in consequence of pressure from within, for the spaces in the kidneys are described as being choked with phagocytes. What appears to have happened is, that the nephrostomes having been stopped up with an accumulation of phagocytes, the pores broke open, and the remaining phagocytes were there expelled, some of them, however, passing into the exposed connective tissue round the edge of the rupture. Another previous experiment by Schneider gives further evidence on the subject.* He made a copious injection of carmine suspended in sterilised salt solution into the body-cavity of *Salmo fario*. His specimens may have been immature; in any case, unlike some of Weber's, they had no abdominal pores. But potentially, I am inclined to think, they were present, as the phagocytes which had engulfed the injected pigment collected at the posterior end of the body-cavity, where the abdominal wall on each side of the anus is very thin. Some of the phagocytes wandered into this thin wall, and in one case they passed right through it and formed a mass of pus on the external surface. This gives, I take it, a very plain hint of what would have happened if the abdominal pore had been present. There would have been no obstacle to the excretion from the peritoneal cavity of the foreign matter and products of inflammation.

The abdominal pores are then excretory ducts, and (should occasion arise) would, as Günther suggested, aid in removing stray ova and semen from the body-cavity as a part of their work, but by no means as the whole of it. And if this view is correct, the body cavity of fishes and of the lower Amphibia is to a great extent an excretory organ, as it certainly is in the early stages of the

* 'Mém. Ac. Imp. Sci.,' St. Petersbourg, [8], 1895, vol. 2, No. 2.

development of almost all Vertebrates. This is in agreement with the result arrived at by van Wijhe in a totally different way, which states that the abdominal pores were excretory ducts and the body-cavity the most primitive excretory organ, functioning as such before the pronephros arose.* It would follow that the abdominal pore is phylogenetically older than pronephric and mesonephric segmental tubes and ducts, and Balfour's homology of the abdominal pores with a posterior pair of segmental tubes would fall to the ground. Without committing myself to van Wijhe's way of regarding the abdominal pores and pronephros, I must say that there is very little to be alleged in favour of Balfour's homology. The arguments with which Balfour† supports his view are rather scanty, amounting to the statement that the pores, for reasons given, are not Müllerian ducts, and that the blind pockets (cloacal pouches) of Selachians are very like primitive involutions from the exterior to form the external openings of a pair of segmental organs. It is now known that the peritoneal end of segmental tubules is formed, especially in Selachians, in a perfectly definite manner from a definite part of the myotome, the dorsal portion of that part which does not form the myomere or muscle segment. Until it is shown that the abdominal pores arise from a corresponding portion of a myotome they cannot be homologised with segmental organs. Their late appearance in many cases, their ventral position, the fact that they are formed (in *Scylium* for instance) at the extreme tip of the peritoneal cavity as a prolongation of that cavity ventrally into the cloacal papilla, that they open at or near the tip of the papilla and not into the bottom of the cloacal pouch, all these facts make it seem unlikely that Balfour's suggested homology will eventually be proved.

The problem naturally arises, which is the primitive condition in Elasmobranchs, that where nephrostomes alone are present, or that where abdominal pores alone are present in the adult? This point cannot, I think, be decided without more evidence.

At first sight it might seem that the persistence of nephrostomial tubes in the adult Selachian was primitive, as these organs are formed at an early stage, in a primitive manner, and are hence phylogenetically ancient structures. Cestracion, moreover, which has this feature, is one of the most primitive of living Selachians. But against all this it may be urged that just as the nephrostomes in adult Amphibia are in all probability a neotenic character, in a group which shows so strong a proclivity to neotenia, so may the retention of open nephrostomes in adult Selachians of the present day be a neotenic phenomenon. This is the more probable, since the nephrostomes in animals which lose them generally disappear at a

* 'Arch. f. Mikr. Anat.', vol. 33, p. 507.

† Memorial Edition, vol. 1, p. 153.

very early age and they are so lost in the Cyclostomata. It is, therefore, not clear whether that intermediate group of Selachians which has both nephrostomes and abdominal pores is on the way to lose the former and depend on the latter or *vice versa*.

With regard to the homology of the pores in the different groups of fishes and in reptiles, the answer will depend on the proof or dis-proof of Balfour's homology. If the pores are not segmental tubes, they are simply perforations of the abdominal wall in consequence of gradual thinning down in the cloacal region. Should this be so, it is evident that this process may have taken place independently many times over in the phylogeny of the different groups, and there would be great difficulty in establishing the homology between any two groups of Vertebrates in respect to the pores.

Let us glance for a moment at the *rôle* played by the body-cavity in the series of changes from its original condition (i) as a part of the excretory system, (ii) as a part of the reproductive system receiving the genital products as they are set free, and (iii) as a part of the lymphatic system, receiving the transudations of the visceral and abdominal walls. From this condition it has been specialised, losing first the sexual part of its duties, when the ovaries and testes became more or less continuous with their ducts. It would afterwards, as in the Anura, become less an excretory organ and more a lymph reservoir, and similarly in the higher reptiles and mammals it becomes more and more specialised as a part of the system of lymphatics.

I must record my gratitude to Mr. Boulenger for facilities granted in examining specimens under his charge at the British Museum, to Mr. S. F. Harmer, Superintendent of the Museum of Comparative Anatomy, Cambridge, for the use of specimens in the collection, and lastly, I owe much gratitude to Dr. Hans Gadow, for the encouragement and suggestive assistance he has always been ready to give me.

Summary.

1. There is a reciprocal and compensating correlation in the adult Elasmobranchii, Ganoidei, Dipnii, some Teleostei, Amphibia, certain Chelonia and Crocodilia in the distribution of nephrostomes and of abdominal pores. In some Selachians only are both present. In the majority of the Elasmobranchii, and in all the other groups, the presence of one set of organs excludes the presence of the other. In the higher Teleostei, in Hatteria, some Crocodiles and Chelonians, both have been lost. Anura hold an intermediate position in so far as the nephrostomes are present, but are no longer connected with the renal system, and the body-cavity communicates with the circulatory system through two channels, (1) through the nephrostomes,

and (2) through stomata. The latter alone form a communication between the body-cavity and the lymphatic system in the Saurii, and Mammalia which have neither abdominal pores nor nephrostomes.

2. If stomata should not be present in the Teleostei and certain Reptilia mentioned above, they would form the only exception to the generalisation that the body-cavity of Vertebrates is never completely closed.

3. The function of the abdominal pores is the same as that of the nephrostomes, viz., the voiding of waste products from the body-cavity.

4. The body-cavity in Pisces and the lower Amphibia is to a great extent an excretory organ.

5. The bulk of the available evidence does not favour the view that the abdominal pores represent a pair of segmental tubules.

6. They seem to be simple perforations of the abdominal wall, and in this case would not necessarily be homologous in the various groups of Vertebrates.

List of the principal Books and Papers referred to above.*

J. Anderson, "On the Cloacal Bladders and on the Peritoneal Canals in Chelonia," 'Linn. Soc. Journ.,' vol. 12, 1876, p. 434.

H. Gadow, "Remarks on the Cloaca and on the Copulatory Organs of the Amniota," 'Phil. Trans.,' B, vol. 178 (1887), pp. 5-37.

A. Günther, "Description of *Ceratodus*," 'Phil. Trans.,' vol. 161 (1871), p. 549; "An Introduction to the Study of Fishes," 1880, p. 123.

J. Hyrtl, "Beiträge zur Morphologie der Urogenital-Organe der Fische," 'Denkschr. k. Akad. Wiss. Wien,' vol. 1, 1850, p. 391; Ueber den Zusammenhang der Geschlechts- und Harn-Werkzeuge bei den Ganoiden," 'Denkschr. k. Akad. Wiss. Wien,' vol. 8, 1854, p. 65; "Anatomische Mittheilungen ueber *Mormyrus* und *Gymnarchus*," 'Denkschr. k. Akad. Wiss. Wien,' vol. 12, 1856, p. 1.

H. F. E. Jungsersen, "Die Embryonalniere des Störs (*Acipenser sturio*)," 'Zool. Anz.,' Jhg. 16, p. 464; "Die Embryonalniere von *Amia calva*," 'Zool. Anz.,' Jhg. 17, 1894, p. 246.

Joh. Müller, "Ueber den Bau und die Grenzen der Ganoiden," 1846; "Fernere Bemerkungen über den Bau der Ganoiden," 'Sitz. Ber. Akad. Wiss. Berlin,' 1846, p. 74.

M. Nussbaum, "Zur Kenntniss der Nierenorgane," 'Arch. f. Mikr. Anat.,' vol. 27, p. 466, 1886.

R. Owen, "Description of *Lepidosiren annectens*," 'Linn. Soc. Trans.,' vol. 18, 1841, p. 343.

W. N. Parker, "On the Anatomy and Physiology of *Protopterus annectens*," 'Roy. Irish Acad. Trans.,' vol. 30, 1892, p. 109.

F. Schweigger-Seidel and J. Dogiel, "Ueber die Peritonealhöhle bei Fröschen und ihren Zusammenhang mit dem Lymph-gefäßssysteme," 'Ber. Sächs. Ges. Wiss. Leipzig,' vol. 18, p. 247, 1866.

* References already given in the text are not repeated here.

J. W. Spengel, "Das Urogenitalsystem der Amphibien," 'Arb. a.d. Zool.-zool. Inst. Würzburg,' vol. 3, pp. 1—114, 1876.
 H. Stannius, 'Handbuch der Anatomie der Wirbelthiere' (2te Auflage), I. Buch. Die Fische, 1854.
 W. Turner, "On the Pori Abdominales of some Sharks," 'Journ. Anat. Phys.,' vol. 14, p. 101, 1879.
 M. Weber, "Die Abdominalporen der Salmoniden, nebst Bemerkungen über die Geschlechtsorgane der Fische," 'Morph. Jahrb.,' vol. 12, pp. 366—406, 1886.

"On the Calculation of the Coefficient of Mutual Induction of a Circle and a Coaxial Helix, and of the Electromagnetic Force between a Helical Current and a Uniform Coaxial Circular Cylindrical Current Sheet." By J. VIRIAMU JONES, F.R.S. Received November 12,—Read December 9, 1897.

(Abstract.)

§ 1. Let M_Θ be the coefficient of mutual induction of a circle and a portion of a coaxial helix, beginning in the plane of the circle and of helical angle Θ . Then if M is the coefficient of mutual induction of the circle, and any portion of the helix for which the extreme points are determined by helical angles Θ_1 and Θ_2 , we have

$$M = M_{\Theta_2} - M_{\Theta_1}.$$

It will therefore be sufficient to show how to calculate M_Θ for all values of Θ .

Let the equations to the circle and coaxial helix be

$$\left. \begin{array}{l} y = a \cos \theta \\ z = a \sin \theta \\ x = 0 \end{array} \right\} \quad \left. \begin{array}{l} y' = A \cos \theta' \\ z' = A \sin \theta' \\ x' = p\theta' \end{array} \right\}.$$

Then it has been shown by the author* that M_Θ may be expressed by the following series which is convergent if $x < A - a$

$$M_\Theta = \Theta(A+a)c^2 \sum (-1)^{m+1} \frac{1.3.5.\dots(2m-1)}{2.4.6.\dots2m} \frac{1}{2m+1} \left(\frac{x}{A+a} \right)^{2m} P_m,$$

where $c = \frac{2\sqrt{Aa}}{A+a}$, $x = p\Theta$,

$$P_m = \int_0^{\frac{\pi}{2}} \frac{\cos 2\theta d\theta}{(1 - c^2 \sin^2 \theta)^{\frac{2m+1}{2}}}.$$

* 'Phil. Mag.,' January, 1889.